OCCURRENCE, HABITAT USE AND MOVEMENTS OF THE FLYING SQUIRREL IN HUMAN-MODIFIED FOREST LANDSCAPES

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Table of contributions

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Original idea	IKH	MJ, OO	**SM**, IKH	IKH, **SM**
Study design	IKH, MS, **SM**	MJ, OO	**SM**, IKH	**SM**, IKH, VS
Empirical data	**SM**, MS	MJ, **SM**	**SM**	**SM**, IKH, VS
Analyses	**SM**	MJ, OO, **SM**	**SM**, OO, HK	**SM**
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ABSTRACT

In recent decades the occurrence and space use of animals in different landscapes have been extensively investigated because of human-driven alterations in native habitats. Especially high detrimental anthropogenic impacts have been recorded in forested ecosystems that have been lost and fragmented. Forest-dwelling animals are generally susceptible to habitat loss and fragmentation because of their strict habitat requirements and dependency on forests for food, nest sites and movements. Consequently, forest specialists, such as arboreal squirrels and gliding mammals, provide a worthy group of model species on which to investigate the effects of landscape modification.

In this thesis, I study occurrence and space use of the Siberian flying squirrel (*Pteromys volans*) in different modified forest landscapes. The flying squirrel is an arboreal rodent inhabiting spruce-dominated mature forests and due to destruction of its most suitable breeding habitat, the population has been declining in Finland. In particular, I investigate which factors are important in explaining its presence in a partly urbanized landscape. In addition, the effectiveness of current habitat protection procedure that is run by regional environmental authorities is assessed. Movement patterns are examined as a response to landscape composition at different scales in urban forests. It is also asked whether flying squirrel survival varies with regional conditions and with individual space use and habitat characteristics.

Flying squirrel occurrence in an urbanized landscape in eastern Finland was positively associated with the amount of forests that are suitable for movements and negatively associated with the isolation of the occupied sites. While I did not find a significant effect of the suitable breeding habitat or a negative effect of the urbanization on the occurrence probability, it seems the species is not heavily disturbed by the urbanization.

We found that the regional environmental authorities are usually unaware of the occurrence of the flying squirrel. Moreover, despite the delineation of the occupied sites according to the given guidelines, protected sites became deserted after forest harvesting. This suggests that the legal protection of the species habitat is ineffective and larger areas of forests should be maintained around inhabited sites to improve conservation implementation.

Urbanized habitats on movement routes increased movement distance and speed whereas similar habitats within the home-range indicated to impede male movements. The importance of structural forested connections remained unclear as the effects of different connections on nest-site switching were varying. This leads to the conclusion that defining and maintaining connectivity in a species-specific way is challenging in human-modified landscapes. Survival of the flying squirrel showed a strong regional variation that could be associated with predation pressure, predator community and landscape composition. Low-quality habitats in the surrounding landscape increased mortality of males, whereas fine-scale habitat structure did not show clear effect. Distances moved by the juveniles during natal dispersal did not increase mortality.

In conclusion, my results indicate that effects of landscape modification on forest-dwelling animals are varying, sex-specific and also depend on the used scale. As landscape modification can affect species indirectly, it is important to investigate the costs and risks of animal movements in human-modified environments.

TIIVISTELMÄ

Ihmisen maankäytön aiheuttamien haitallisten maisemamuutosten takia eläinten tilankäyttöä ja esiintymistä erilaisissa maisemissa on tutkittu kattavasti viimeisten vuosikymmenien aikana. Ihmistoiminta on vähentänyt ja pirstonut etenkin metsäisiä elinympäristöjä. Metsälajit ovat yleensä herkkiä elinympäristömuutoksille niiden tiukkojen elinympäristövaatimusten takia ja koska ne ovat riippuvaisia metsistä ravinnon, pesäpaikkojen ja liikkumisen suhteen. Siksi metsiin erikoistuneet lajit, kuten puissa elävät oravat tai liitävät nisäkkäät, ovat sopivia mallilajeja maisemamuutosten vaikutusten tutkimuksessa.

Selvitän väitöskirjassani liito-oravan (*Pteromys volans*) esiintymistä ja elinympäristön käyttöä ihmisen muokkaamissa metsämaisemissa. Liito-orava on varttuneisiin kuusisekametsiin sopeutunut laji, joka on kärsinyt sopivien elinympäristöjen vähenemisestä ja Suomen kanta on arvioitu laskevaksi. Tarkemmin tutkin lajin esiintymiseen vaikuttavia tekijöitä nimenomaan kaupunkimaankäytön pirstomalla tutkimusalueella. Tarkastelemme myös lajin suojelun vaikuttavuutta nykyisen suojelukäytännön kautta. Lisäksi selvitän radioseurannan avulla kaupunkimaiseman vaikutusta liito-oravan liikkeisiin ja elinympäristönvalintaan eri mittakaavoissa ja myös tutkimusalueen maisemakoostumuksen ja yksilöllisten ominaisuuksien vaikutusta liito-oravan selviytymiseen.

Liito-oravan esiintymiselle kaupunkimaisemassa on olennaista tarjolla olevan liikkumiseen soveltuvan metsäympäristön määrä sekä etäisyys lähimpään liito-oravaesiintymään. Varttunut kuusisekametsä ei kasvattanut eikä kaupunkimainen elinympäristö vähentänyt lajin esiintymistodennäköisyyttä mikä viittaa siihen, että liito-orava ei kärsi kaupungistumisesta, jos sopivaa elinympäristöä on saatavilla.

Havaitsimme, että tieto liito-oravien esiintymisestä on puutteellista alueellisten ympäristöviranomaisten keskuudessa ja metsänkäsittelyn yhteydessä jätettävät suojelualueet eivät turvaa lajin pitempiaikaista säilymistä. Lajin elinympäristönsuojelu nykykäytännön mukaan on tehotonta ja suojelutason parantamiseksi vaadittaisiin suurempia metsäisiä alueita esiintymän ympärille.

Kaupunkielinympäristön osuus liikkumisreittien varrella kasvatti yksilöiden liikkumia etäisyyksiä ja liikkumisvauhtia. Jos otettiin huomioon saman elinympäristötyypin osuus koko elinpiirin sisällä, se vähensi etenkin liito-oravakoiraiden öisiä liikkumismatkoja. Pesäpaikkojen välisten puustoisten yhteyksien tärkeys jäi epäselväksi ja päättelemme, että maiseman kytkeytyneisyyden määrittely ja säilyttäminen on haastavaa etenkin ihmisen muokkaamissa metsäympäristöissä. Liito-oravan eloonjäämisessä on huomattavaa alueellista vaihtelua, joka johtuu erilaisesta maisemakoostumuksesta, saalistuspaineesta ja petoyhteisöstä. Huonolaatuisten elinympäristöjen määrä ympäristössä lisäsi koiraiden kuolleisuutta, kun taas eniten käytettyjen alueiden elinympäristökoostumuksella ei ollut vaikutusta. Myöskään nuorten liikkumat matkat uusille elinalueille levittäytymisen aikana eivät lisänneet niiden kuolleisuutta.

Tutkimustulokseni osoittavat, että maisemamuutosten vaikutukset metsälajeihin ovat vaihtelevia ja voivat riippua myös sukupuolten välisistä eroista tilankäytössä sekä käytetystä mittakaavasta. Maisemamuutokset voivat siten vaikuttaa lajeihin myös epäsuorasti ja siksi on tärkeää selvittää eläinten liikkumisen kustannuksia ja riskejä ihmisen muokkaamissa maisemissa.

SUMMARY

1. Introduction

In recent decades it has been extensively studied how landscape modification affects animal occupancy patterns and space use. This is driven by anthropogenic alterations in native habitats, which are threatening numerous animal species and causing global loss of biodiversity (Baillie et al. 2004). Habitat loss and fragmentation are together the biggest threats for terrestrial mammals worldwide (Schipper et al. 2008). Still, we do not have a comprehensive understanding on the processes at individual or population level that allow existence or cause decline of populations in fragmented landscapes (Banks et al. 2007). Given that human impacts on native habitats will continue, a great part of species conservation will occur not in pristine but in already partly modified environments. It is therefore important for species conservation and landscape management to study responses of animals with respect to changes in their native habitats (Knowlton and Graham 2010).

1.1. Anthropogenic impacts on forests and species conservation

Almost all of the ecosystems have been negatively affected by anthropogenic land use and especially high detrimental impacts have been recorded in forested ecosystems (Lindenmayer and Franklin 2002). During the last decades, the rate of native forest modification has been extensive in tropical and subtropical areas, but boreal forest ecosystems, with the long history of forest management have also been severely altered (Hansson 1992, Gardner et al. 2009). Therefore, old-growth forest specialists have become one of the most threatened groups of mammals in Europe (Mortelliti et al. 2010). In terms of landscape ecology, forest habitats are affected by the loss of habitat and by separate processes related to fragmentation, such as the decreased size and increased isolation of remnant patches (Fahrig 2003). The most straightforward impact on animals is the loss of forest area, which directly decreases the amount of suitable habitat and restricts the number of individuals present (Andrén 1994). However, animals may also be harmed by the loss of connectivity, because isolation of remnant patches and quality of the intervening habitat together with species movement abilities determine if animals are able to move through the landscape (Taylor et al. 1993). Along with fragmentation and decrease in patch size, forest fragments become increasingly dominated by edge habitat. Ecological conditions at edges differ from those of interior habitats and influence animals either positively or negatively through species interactions or resource availability (Fahrig 2003, Ries et al. 2004). For example, negative edge effects are caused by when the predation risk in

the edge habitat increases or edges restrict movements for a given species (Lidicker 1999, Chalfoun et al. 2002).

Humans modify native forest landscapes mainly through agriculture, forestry and urban land development (Foley et al. 2005). Unlike natural disturbance on forests, created by fire or insects, human disturbance creates adjacent non-forested ecosystems where ecological conditions differ from the natural forest ecosystems (Ries et al. 2004, Harper et al. 2005). In addition, human-made boundaries are often linear and result in simple shapes (Forman and Alexander 1998). Conversion of native forests to commercial forests typically leads to temporally dynamic and mainly forested landscape mosaic where forest stands differ in their tree species composition and age, and where contrast of habitat edges is affected by succession or regeneration by forest practise (Schmiegelow and Mönkkönen 2002). For example, clearcuttings that have the strongest isolation effect are considered to be the most detrimental of the different management practices (Prugh et al. 2008, Franklin and Lindenmayer 2009). On the contrary, urban and agricultural land use produces landscapes with high-contrasting and long-lasting edge effects and obvious remnant forest fragments (Didham and Lawton 1999, Harper et al. 2005). Urban landscape is in general heterogeneous, heavily fragmented, and characterized with several kinds of land-use types such as different residential and urban land cover classes (Luck and Wu 2002). Thus, responses of species to habitat changes can vary with the entire landscape context (Mönkkönen and Reunanen 1999).

In addition to direct impacts on forested habitats, human presence and infrastructure can indirectly change living conditions and mortality risks for forest-dwelling species. Furthermore, human-introduced 'novel' predators can induce higher predation pressure, light pollution can bring additional stress and collisions with buildings or vehicles increase animal mortality in cities (Ditchkoff et al. 2006, Chace and Walsh 2009). On the other hand, not every species suffers from anthropogenic land use and human presence; it is possible that some generalist predators take advantage of the fragmented landscape, or alternatively, species resistant to habitat changes can benefit from side-effects of urbanization, such as increased food resources or fewer natural predators (McKinney 2002, DeStefano and DeGraaf 2003).

There is several ways on how to mitigate the negative effects of habitat loss and fragmentation in modified landscapes (Marzluff and Ewing 2001) and it is important to identify the main threats for particular species or species-assemblage and plan a conservation strategy accordingly. Consequently, conservation implementation depends on whether one attempts to protect a single species or a group of species (Fischer and Lindenmayer 2007). Thus, in habitat protection for a given species means have been in conservation of habitat patches that are large enough for species persistence and in maintenance of connectivity of the landscape by corridors or stepping stones when

habitat is fragmented (Soulé 1991, Marzluff and Ewing 2001). However, there has been great controversy in determining which is more important; preserving habitat area or maintaining connectivity (Franklin and Lindenmayer 2009). Large and intact forest patches indisputably protect biodiversity and benefit many species (Andrén 1994). However, it has been found that the interspersed land cover, i.e. non-habitat matrix (hereafter matrix) determines how sensitive a species is to effects of patch size and isolation (Prugh et al. 2008). The effectiveness of corridors has also been disputed (Simberloff et al. 1992, Beier and Noss 1998). Although forested corridors can promote animal movements, results on corridor utility are conflicting because certain types of corridors seem to benefit only some species (Andreassen et al. 1996, Haddad et al. 2003). It has been shown that by carefully planned forest corridors, movements of relatively strict habitat specialists can be facilitated (Beier and Noss 1998). However, species that are able to use a matrix may benefit from matrix management and it may be a more cost-efficient tool to improve connectivity (Caryl et al. 2012). Since a matrix can provide additional habitat and resources, it is possible that a high-quality structurally complex matrix benefits a larger amount of species (Brady et al. 2011). Overall, all the previous observations suggest that protection of animals in modified landscapes is challenging and depends on species-specific resource requirements and movement abilities.

1.2. Arboreal squirrels and gliding mammals as model species

Forest-dwelling species are considered susceptible to landscape modification due to their strict habitat requirements, dependency on forests for moving, food and nest sites and unwillingness to cross gaps in the forest cover (Koprowski 2005, McAlpine et al. 2006, van der Ree et al. 2010). Consequently, habitat loss and fragmentation are threatening many forest-dwelling mammalian species in different parts of the world (Lindenmayer et al. 2000, Mortelliti et al. 2010). For example, tree squirrels, which are widely distributed across forested ecosystems, differ greatly in their sensitivity to habitat changes (Koprowski 2005). Furthermore, a specific group of forest-dwelling mammals consists of arboreal squirrels and marsupials, which move by gliding and thus are potentially harmed by specifically loss of forest connectivity as they might be restricted by their maximum gliding distances (van der Ree et al. 2004). Arboreal squirrels and gliding mammals together provide a worthy group of model species on which to study the effects of forest loss and fragmentation. In addition, some of them can be used as indicators of forest quality or umbrella species to protect forest biodiversity (Koprowski 2005, Hurme et al. 2008b, Mortelliti et al. 2009).

Landscape composition has often been found to be an important factor in explaining the occurrence of squirrels and gliding mammals in different landscapes, whereas the results on the importance on landscape configuration (i.e. structure) have been mixed

(Lindenmayer et al. 2000, Ritchie et al. 2009). Thus, a positive effect of suitable forest area has been significant in many studies, but effects of habitat fragmentation have remained less clear (Verbeylen et al. 2003b, Patterson and Malcolm 2010). However, in some cases, presence of a species has been restricted to fragments that lie within the maximum gliding distance of the species (van der Ree et al. 2004). In addition, connectivity and quality of the matrix have proven to be important predictors of species occurrence in urbanized landscapes (Verbeylen et al. 2003a, Caryl et al. 2013). Some species are affected by all of these aspects. As an example, the occurrence probability of Siberian flying squirrel (*Pteromys volans*) has been associated both with the forest patch size and the availability of important resources, and additionally with distance to the nearest occupied site or with the presence of forested connections (Reunanen et al. 2002, Hurme et al. 2007, Santangeli et al. 2013a). Nevertheless, it is evident that the occupancy patterns are in line with the ability of the species to move through the modified landscape (Fahrig 2003, Tischendorf et al. 2003).

In general, habitat fragmentation is expected to decrease the overlapping of home ranges as habitat patches for a species become isolated, or to expand the home ranges when individuals include more suitable patches to acquire all the needed resources, or to decrease the size and increase the aggregation of home ranges (Ims et al. 1993, Banks et al. 2007). Space-use responses of arboreal squirrels and gliding mammals have shown variation with landscape structure; compaction response has been detected when home-ranges of species are smaller in fragmented areas, in linear remnants and in edge areas of forests (Wauters et al. 1994, van der Ree and Bennett 2003, Verbeylen et al. 2009, Brearley et al. 2011a). For example, home ranges for fox squirrel (*Sciurus niger*) and grey squirrel (*Sciurus carolinensis*) increased with a forest patch size, whereas red squirrel (*Sciurus vulgaris*) showed no clear response (Koprowski 2005). Fragment size has influenced the probability to leave a patch, being greater in smaller patches (Selonen and Hanski 2003, Rizkalla and Swihart 2007). In addition to species-specific patterns, sex-specific space-use patterns have been observed and have found to be related to sex-specific area requirements, territoriality or defence of high-quality core areas (Verbeylen et al. 2009). For example, home ranges of flying squirrel males have expanded in relation to fragmentation whereas females have typically stayed within one forest fragment (Selonen et al. 2001, Taulman and Smith 2004).

Landscape structure can also affect small-scale movement patterns and tree squirrels and gliding marsupials have showed various responses to edges and landscape matrix: movements through clearcuttings and unsuitable matrix have been faster and straighter, and lengths of movements have increased in fragmented landscapes (Selonen and Hanski 2003, Smith et al. 2013). Urbanization of landscape matrix can also hinder movements (Caryl et al. 2013). Responses to edges can depend on distance to the edge and edge

contrast, but for example flying squirrels have not shown any avoidance of edges when they are active in the night time (Desrochers et al. 2003). It also seems that tree squirrels readily cross gaps in forest cover and movement decisions have been related to detour efficiency, for example red squirrels seem to be able to assess costs or risks of alternative routes (Bakker and Van Vuren 2004). Corridors do not seem to be essential to ensure movements, at least for the flying squirrel species, as they have been used when available but also matrix habitat has been used for movements and foraging (Selonen and Hanski 2003, Taulman and Smith 2004).

Existence of populations and redistribution of individuals in modified landscapes are generally associated with successful dispersal (Clobert et al. 2012). Moreover, dispersal distance is theoretically expected to have costs, which may vary with landscape modification (Bonte et al. 2012). Dispersal-type movements have been mainly studied with flying and tree squirrel species. For example, dispersal movements for flying squirrels have become longer with landscape fragmentation and facilitated by landscape connectivity (Selonen and Hanski 2004, Smith et al. 2011). Furthermore, natal dispersal, terminal movement from the natal site to establish an own territory, has been habitat- or sex-biased in flying squirrels and red squirrels (Haughland and Larsen 2004, Selonen et al. 2007, Hanski and Selonen 2009), although habitat fragmentation has been demonstrated to harm selection of alike settlement sites (Wauters et al. 2010). It seems that habitat use of dispersing juveniles differs from habitat use of adults (Bowler and Benton 2005); for example, flying squirrel juveniles preferred the most suitable breeding habitat but in comparison with adults they used more matrix and moved longer distances through unsuitable habitats (Selonen and Hanski 2006).

Finally, in spite of the diversity and flexibility of animal behaviour and movements in modified landscapes, living in these kinds of environments is not without costs (Fahrig 2007). In fact, survival of local populations has been linked to loss and fragmentation of their native habitats (Lampila et al. 2009, Koskimäki et al. 2014). Mortality may be higher because of increased predation risk and more diverse predator community in fragmented landscapes or increased mortality during movements in risky and unsuitable habitats (Ries et al. 2004, Ryall and Fahrig 2006, Fahrig 2007). Moreover, habitat in modified landscapes can act as ecological traps, such that individuals are settling to habitat fragments that seem to be of good quality, but eventually increase mortality of the population (Battin 2004).

1.3. Siberian flying squirrel and its conservation challenge

The national population of the Siberian flying squirrel has been monitored since 2003 in Finland and it has been declining due to ongoing loss of the most suitable breeding habitat, mature spruce-dominated forest, by forest management practices (Hokkanen et

al. 1982, Hanski 2006). Habitat loss have proven to result in decreased size and survival of local populations (Lampila et al. 2009, Koskimäki et al. 2014). Because of the observed population decline, this species is recently categorized as nearly threatened in Finland (Liukko et al. 2015), although globally the status is least concern (Shar et al. 2008). The breeding and resting places of the species are protected in the European Union Habitats Directive, and forest management guidelines have been given when the species is found at the time of a forestry procedure (Anonymous 2002; 2004). To date, it has been the task of regional environmental authorities of Finland (Centers for Economic Development, Transport and the Environment) to monitor and delineate the resting and breeding places prior to forest management action. It has also been found that current level of habitat protection is not effective (Santangeli et al. 2013b). Thus, presence of the flying squirrel has been conflicting with forest management and land-use planning in many areas. Even though the flying squirrel is considered a specialist of reasonably intact old-growth forests, recent observations show that it can occupy urban landscapes if suitable breeding habitat is available.

1.4. Aims of the thesis

In this thesis I aim to find out how flying squirrels are adapting to urban environments and whether they are influenced by landscape structure and living conditions in partly urbanized and other modified forest landscapes. Observations of flying squirrel have been made near human settlements and cities despite its preference for mature and relatively undisturbed forests, and this arises a question on whether flying squirrels are able to successfully live in urban forests. Initially, it is important to investigate which factors generally influence the presence of flying squirrel in the urban landscape. Thus, in chapter **I**, I study what landscape characteristics explain the presence of the species on a local scale in a partly urbanized area in Eastern Finland. I aim to test whether flying squirrel is occurring in the near vicinity of residential areas or whether it is negatively affected by urbanization of the landscape.

In the light of the global biodiversity loss, the national population decline of the flying squirrel and conflicts between flying squirrel protection and forest management, we study the effectiveness of current habitat protection procedure in chapter **II**. This is investigated through two separate study questions. First, we use a simulative approach to examine how often the delineation of nesting and resting places of the species does not occur because the presence of flying squirrel is unknown to authorities. Second, we investigate that when protection is implemented according to current guidelines, how often it results in effective conservation of the species, meaning that the occupancy of previously inhabited site continues after delineation decision and forest harvesting.

As a tree-dependent species the flying squirrel is potentially affected by changes in the forest landscape. However, little is known about its spacing behaviour and movements, particularly in urbanized areas. Therefore, there is a need to improve our knowledge on its habitat requirements in these modified landscapes. In chapter **III**, I examine the effects of landscape composition on home-range use and movement activity of flying squirrels. In particular, I investigate the effects of habitat availability on movement distances and movement speed on different scales. I analyze whether the structural connectivity between nest sites affects the nest-switching probability.

It is likely that flying squirrel occupancy and movement patterns are affected by the decrease in the amount of mature forests, but observations of individual survival are deficient in modified landscapes. Desertion of occupied sites may be caused, for example, by mortality of the individual because of increased predation pressure or lack of resources, or by a behavioral response such as abandoning the low-quality site. Thus, in chapter **IV** I study how survival of individuals is influenced by habitat availability and landscape modification. In addition, survival estimates of study areas that differ in their landscape composition and degree of urbanization are compared, and the effects of individual properties such as sex, age or natal dispersal distance that can cause variation in survival are examined.

2. Material and Methods

2.1. Biology of the Siberian flying squirrel

The Siberian flying squirrel is a nocturnal and arboreal small-sized rodent distributed across the Eurasian boreal forest zone from Finland to the Korean Peninsula and Japan (Wilson and Reeder 2005). Its most suitable breeding habitat in Finland are mature coniferous forests dominated by the Norway spruce (*Picea abies*) with a component of deciduous trees such as alders (*Alnus glutinosa* and *A. incana*), aspen (*Populus tremula*) and birches (*Betula pendula* and *B. pubescens*) (Hanski 1998, Reunanen et al. 2002). Flying squirrel nests in cavities that are either natural or made by woodpeckers (*Dendrocopos major* and *Picoides tridactylus*) and mostly in aspen. It can also roost in twig-nests made by the red squirrel, or in structures of buildings or nest boxes (Hanski et al. 2000a). During late fall, winter and early spring flying squirrel consumes buds and catkins of alder and birch, and buds of spruce and pine. In summer it is mostly eating leaves of various deciduous trees (Hanski et al. 2000b).

Adult individuals are site-tenacious and spacing behaviour differs between sexes. Females defend their non-overlapping territories (on average 6.5 ha) whereas males occupy extensive home ranges of on average 65 ha. Territories of males often overlap with each other and can also contain several female territories (Selonen et al. 2001). The flying squirrel mating system is promiscuous and the mating season is between March and mid-May including two estruses of females during which copulations take place (Selonen et al. 2013). Thus, the first litter is born in the end of April and the second in June. Natal dispersal of juveniles occurs between mid-July and September, the majority of females and about 60% of the males disperse (Hanski and Selonen 2009). Dispersal distances have been on average 2.5 km for females and 1.8 km for males.

2.2. Study areas

Most of the data for this thesis (**I, III, IV**) was collected in a partly urbanized study area in Kuopio, Eastern Finland (Figure 1, a, enclosed by rectangle). For chapter **II**, we gathered comprehensive occurrence data on five additional areas to study how often presence of the species is unknown to the authorities (Figure 1, a, grey circles). In order to study the effectiveness of habitat protection, we used occurrence data on 100 breeding and resting places that were delineated by the regional environmental authorities in the central and southern part of the country (Figure 1, a, area approximated by a dashed dark grey line). In chapter **IV**, I included data from three other study areas (Figure 1, a, white triangles) from southern Finland, where flying squirrels were monitored earlier.

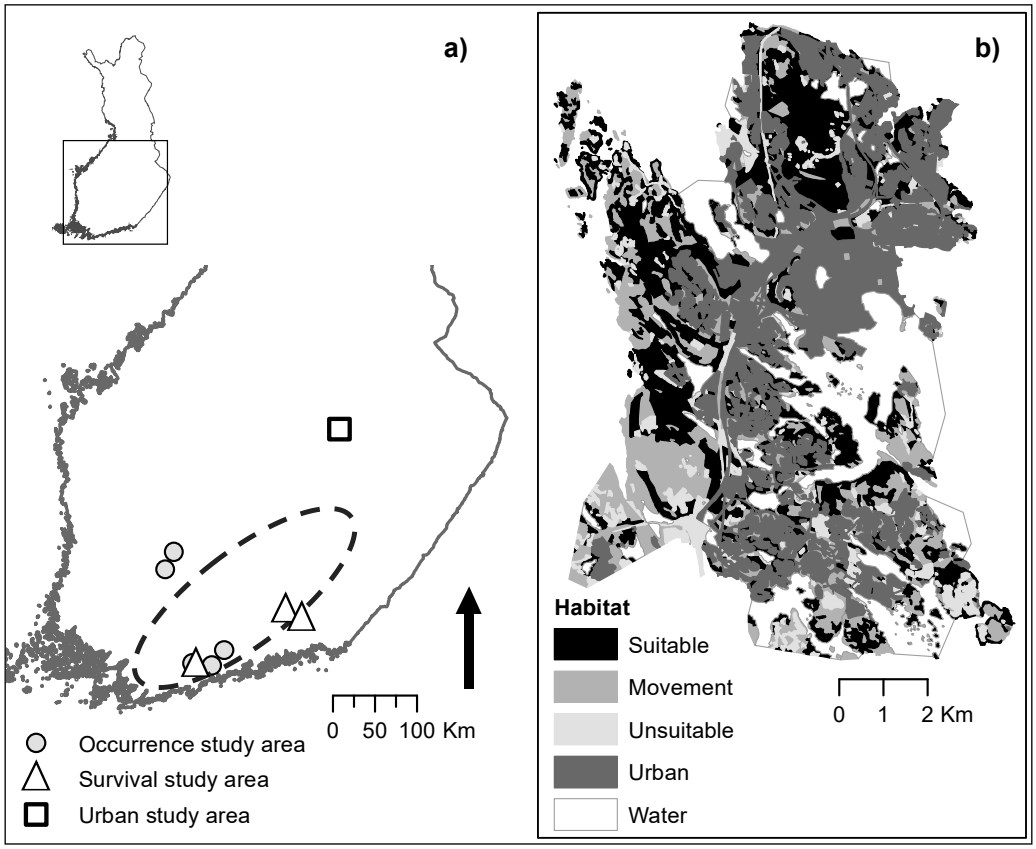

Fig. 1 a) Locations of study areas in southern part of Finland. Grey circles represent the areas (n = 5) where data was collected and simulated to get the proportion of flying squirrel presence unknown to authorities. Data on the effectiveness of the delineation practice in case of forest harvesting was collected from 100 breeding and resting places within the large dark grey dashed circle (chapter **II**). Radio telemetry for studying flying squirrel survival (chapter **IV**) was conducted within three study areas denoted by white triangles and within the urban study area (enclosed by rectangle), where also home-range use of urban flying squirrels was monitored. Urban study area was also surveyed for pellets and the occurrence data was used for chapters **I** and **II**. **b)** Landscape composition of the urban study area in Kuopio, Eastern Finland and habitat classification according to suitability for the flying squirrel.

Landscape composition and topography varied greatly among all of the study areas, but in general, landscapes of the study sites are characterized by a mixture of forests, agricultural and urbanized areas, bogs and water bodies. The dominating tree species in forests were Norway spruce, Scots pine (*Pinus sylvestris*), downy and silver birch, and European aspen. The main study site in Kuopio comprised of about 30% of urban infrastructure and belonged to Northern Savo core area of herb-rich vegetation, hence part of forests were groves or heaths with rich grass-herb vegetation (Ahti et al. 1968). In all study areas, most of the forests were managed and utilized for timber production,

except one survival study site that located in Nuuksio national park, where most of the forests were protected.

2.3. Data collection

The flying squirrel is nocturnal and difficult to observe. A commonly applied method to define the presence of the species in a forested area is to search for its easily recognizable yellowish and rice-grain-shaped faecal pellets at the bases of aspens and mature spruces (Skarén 1978). This method was applied to record the occurrence of the species in chapters **I** and **II**. Surveys were conducted between April and July, during which the detection of pellets is possible. This method has been used during several decades in Finland and it is considered a reliable method with a relatively high detection probability (Hurme et al. 2008a, Santangeli et al. 2013a).

In order to investigate habitat use and survival of the species (**III-IV**), I used radio tracking of collared individuals. First, individuals were caught from nest boxes or by plastic tube traps in which they fell after emerging from their cavities after sunset (method described by Hanski 1998). All individuals were weighed and fitted with collars with radio transmitters (Biotrack Ltd.). Catching of adult individuals took place throughout the year whereas juveniles were caught between the end of June and mid-August when they were large enough to be collared. After fitting a collar, the individual was released near its nest tree or placed back inside the nest box. Location of the squirrel was checked during the next day. Radio-collars were not observed to cause any harm for the species.

To study home-range and nest-site use patterns in the urbanized area, I collected radio-tracking data on 44 adult flying squirrels (22 females and 22 males) in Kuopio between 2008 and 2012 (**III**). Flying squirrels are not usually disturbed by the radio tracking procedure, thus they were located as accurately as possible; in a single tree or in a group of trees. Night-time radio tracking took place from March until the end of September. Following of nightly movements was started after sunset and each individual was followed for 0.5 to 2 hours. In the beginning of the field season individuals were resting in the nest in the middle of the night, and thus movements were followed both during the late evening and during early morning hours. Individuals were monitored throughout the short nights in summer. To define the use of daytime nesting places, locations of individuals were checked in daylight at least once per week during the field season (March-September) and on average once per month during winter (October-February). All locations with the coordinates and exact timing were saved to a GPS-device.

In the survival analysis, I used statuses of in total 267 individuals that were monitored by radio tracking in the four different study areas between 1997 and 2012 (**IV**). Data

included both night- and daytime check-ups of individuals throughout the year, and checking was more frequent between March and September (at least once per week) than during winter months (on average once per month). Death was confirmed in all cases by finding a dead individual or a collar on the ground. Cause of death was classified to the categories predation, other or unknown.

2.3.1. Landscape variables

Landscape data for this thesis has been mainly produced by creating continuous land cover maps by joining spatial information from different sources. For example, habitat classification for the urban study area was created by combining information on forest stand composition (received from Kuopio City), aerial photographs and field survey, and then categorizing the landscape according to suitability for the flying squirrel into following classes: 1) mature spruce dominated forests with a deciduous tree component and nesting cavities, suitable breeding habitat, 2) other forests that are over 10 m high, for example pure pine or birch forests, suitable movement habitat, 3) treeless or sparsely forested areas like clearcuttings, sapling stands, fields and open bogs, mostly unsuitable for the flying squirrel, 4) urban areas such as residential areas or other urban infrastructure, mostly unsuitable for the species, 5) water bodies that can work as movement barriers (for representation of the classes in urban study area of Kuopio see Figure 1b). This classification was used to study the effects of landscape on movement patterns and survival (**III**, **IV**). Similarly classified and earlier digitized landscape data was used in survival analysis for the three other study areas (**IV**, Selonen et al. 2001, Selonen and Hanski 2006). A more detailed classification where urban areas were divided into dense and newly built residential areas, and residential areas with trees was used in chapter **I**.

To find the factors that would explain occurrence of the species in urban areas, I created random points over the forest land, points that hit for example water or residential areas were excluded, and buffered them by a 400-m radius (**I**). The resulting area (50.2 ha) described the surrounding landscape, and took into account of space requirements of both males and females. Buffered areas were not allowed to overlap over 10% or contain over 35% of water. To find out how often the authorities are unknown of the flying squirrel presence (**II**), landscape data of the chosen study landscapes was created by reclassifying forest age of multi-source national forest inventory data (Metla 2012) into three habitat classes: advanced thinning stands and mature forests, young forests, and unsuitable areas (agricultural and urban areas, water bodies). Proportions of the same habitat types were also measured within a 150-m radius around breeding and resting sites delineated by the environmental authorities at the time of delineation and after forest logging.

Habitat availability of individual flying squirrels was measured at several scales. To quantify the habitat on movement routes, flying squirrel tracks were buffered by a 25-m radius and proportions of different classes were measured within those areas. Similar habitat proportions were measured within 100% minimum convex polygons (MCP) (Harris et al. 1990) to quantify the composition of home range (**III**). When relating surrounding landscape to survival probability, I measured habitat classes that were within a 500-m radius of the central location of a flying squirrel. I used 100% single-linkage clusters (Kenward et al. 2001, Wauters et al. 2007) to describe fine-scale habitat availability (**IV**).

In order to inspect how nest-switching probability of an individual was affected by distance and structural connectivity between nest sites (**III**), I first computed a distance between all nest sites of each individual, and then defined altogether 12 different connectivity measures between each nest site. According to the different connectivity definitions, nest sites were connected either by a straight line, or by taking a detour or by also allowing routes outside the home-range boundaries. Above-mentioned connections were supposed to consist of suitable breeding habitat type only or all forests that were over 10 m high (a combined class of suitable and movement habitats). A similar set of connectivity measures was defined by allowing gaps that flying squirrel were able to cross by one glide (not over 50 m) (Figure 2).

2.4. Statistical analyses

Generalized linear models were used to model the presence and absence of the species at a site in relation to multiple landscape variables (**I**-**II**), and similarly, to study if the number of distinct nests is affected by home-range size or habitat composition of the home range (**III**). In chapter **II**, we used linear regression to estimate the fraction of logging sites that should have been protected, and explained the simulated fraction of final logging sites occupied by the species by the simulated fraction of sites where a species would have been present in the national flying squirrel survey within each of the five study areas.

I conducted linear mixed effect models to investigate the effect of habitat composition on three response variables: length and speed of movement burst and nightly moved distance (**III**). Cox proportional hazard models that correspond with non-parametric regression were used in the survival analysis (Cox and Oakes 1984). To account for repeated measures and possible individual or temporal variation, individual and year were used as random effects of the intercepts when necessary (Zuur et al. 2009). Differences in survival probabilities between different groups were compared by a log-ratio test that was modified to take in account accelerating and crossing survival curves (Harrington and Fleming 1982).

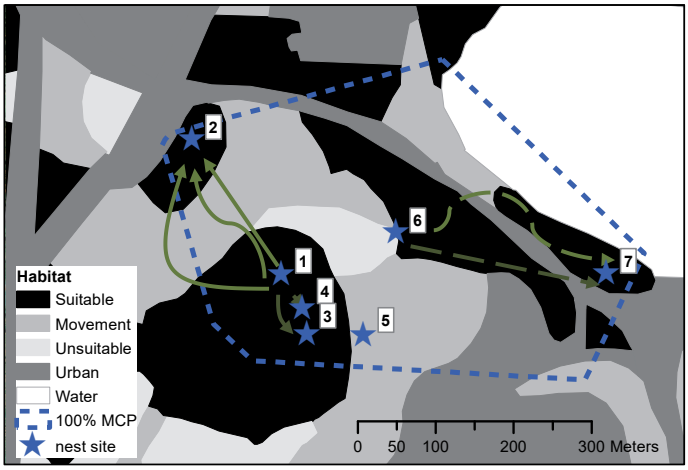

Fig. 2 Example of habitat composition, locations and connectivity of nest sites of a Siberian flying squirrel used to study the home-range use patterns in chapter **III**. A female home range by 100% minimum convex polygon (MCP) is delineated by the blue dashed line and numbered stars denote for the distinct nest sites. Different structural connectivity measures are shown by the arrowed lines. For example, individual could move from nest 1 to nest 2 by a straight line, or tortuously inside or outside home-range boundary, but in all cases the track would also comprise of movement habitat (green arrows). However, if moving between nest sites 1, 3 and 4, all movements fall within the suitable habitat (dark green arrows). In order to move from nest 6 to 7, female could move directly via suitable forest or taking detour, but it had to cross a gap in tree cover (dashed arrows).

To investigate habitat use of flying squirrels during night-time movement period in chapter **III**, I conducted a compositional analysis where proportions of available habitats within home range (100% MCP) were compared to proportions of habitats used during movements (Aebischer et al. 1993). Possible differences between sexes were accounted for by running the analysis separately for males and females. To investigate the effect of distance, connectivity and their interaction on nest-site switching, we used a Bayesian framework and a transition between the nest sites for each individual was modelled using a Markovian chain (**III**). Akaike's Information Criterion and Deviance Information Criterion were used for model selection (Burnham and Anderson 2002, Spiegelhalter et al. 2002).

3. Results and Discussion

Siberian flying squirrel occurrence has earlier been related to regional and local-scale landscape characteristics. However, these studies have been mainly restricted to areas that lie in the northern distribution range of the species (Mönkkönen et al. 1997, Hurme et al. 2007) and studies on space use have been carried out in managed forest landscapes outside cities (Hanski 1998, Hanski et al. 2000a, Selonen et al. 2001). In this thesis, ecological responses of the species in relation to urban conditions were investigated for the first time, and data on other modified forest landscapes were used for comparison. Furthermore, studies were conducted on different temporal and spatial scales. For example, habitat was measured on a small scale within individual movement routes or within small-sized cluster home ranges that describe the most frequently utilized areas by individuals, but also on a larger scale within buffers of several hundred meters to describe the surrounding landscape composition and availability of different habitats.

3.1. Landscape composition and isolation affect the occurrence in urban landscape

In general, species are not randomly distributed across landscape, but are affected by a great amount of factors, such as the availability of suitable habitats, resources and conspecifics or territorial behaviour and interactions with the other species (Banks et al. 2007). Therefore, factors that determine the occurrence of forest-dwelling species in modified landscapes have been widely studied (e g. Mazerolle and Villard 1999, McAlpine et al. 2006, Mortelliti et al. 2010). In the partly urbanized study area in Kuopio, eastern Finland, the occurrence of the Siberian flying squirrel was most affected by the amount of habitat suitable for species movements and by the distance to the nearest occupied site (**I**). More particularly, the movement habitat (forests higher than 10 m) had a positive effect on the probability of presence, whereas the probability decreased with an increasing distance between the occupied sites. The importance of movement habitat indicates that a habitat which facilitates movements of the species through a fragmented landscape promotes species occurrence. Similarly, a semi-suitable forest area had a positive effect on the species presence in managed forest areas around the protected breeding and resting sites (**II**). In addition, the positive effect of movement habitat could be explained with forest types dominated by deciduous trees that are used for foraging, and being included in this habitat (Selonen et al. 2001, Selonen and Hanski 2003). The negative effect of distance is in line with earlier observations of occurrence probability (Reunanen et al. 2002, Hurme et al. 2007, Santangeli et al. 2013a), and it is also supported by the general movement patterns of the species. For example, the average nightly moved distances by males are roughly comparable to the average distance between the occupied sites (776 m).

The flying squirrel presence was not found to be negatively affected by an amount of urbanized habitats (**I**). As evidence, urban habitat variables did not appear to be important in explaining the species occurrence. In addition, I observed that flying squirrels occurred in the edge areas of forests near residential areas and in forest fragments within suburbs. This is in line with the previous observations where flying squirrels were not found to particularly avoid the edge habitats (Desrochers et al. 2003). On the one hand, my results could indicate that squirrels find human influence insignificant, or that they are able to utilize some resources also near the human settlements. For example, some other arboreal species have been found to exist in greater numbers in sites that locate near edges of small roads or residential areas (Brearley et al. 2011b). On the other hand, animals could still exist in the vicinity of recently developed residential areas, as the effect of increased edge habitat and fragmentation can have a time lag. Thus, the population might decline later (Fahrig 2002; 2003). Urban environments have also traditionally been suggested as safe places to many species due to absence or lower number of natural predators (Stochat et al. 2006, Møller 2012). Therefore, in order to confirm the non-negative effect of urbanization, long-term monitoring of the occupied sites is needed.

Occurrence of a habitat specialist is usually linked to the surface area of its most suitable breeding habitat, but landscape configuration, quality of the matrix and the amount of remaining habitat at the landscape scale may confound the effect of most suitable habitat area (Andrén 1994, Fahrig 2003, Ewers and Didham 2006). In contrast to the delineated sites in southern Finland (**II**) and to the earlier studies (Reunanen et al. 2002, Hurme et al. 2007), we did not found any effect of mature spruce-dominated forests within 400-m radius on flying squirrel presence in the urban area in Kuopio. However, more fine-scale habitat variables can also affect the habitat suitability and thus the occurrence of the squirrels. In addition, complex interactions between species or predator avoidance could result in different spatial distribution patterns than expected based on habitat availability. For example, flying squirrel occurrence was not strongly affected by landscape composition or vegetation zone, but the species seemed to avoid the nocturnal predator, the Ural owl (*Strix uralensis*) and exist spatially aggregated with the northern goshawk (*Accipiter gentilis*), when both predators were present (Byholm et al. 2012). Thus, my findings altogether suggest that other factors than the amount of suitable forest at the landscape scale are more important in explaining species presence in an urbanized area.

I observed that isolation, measured as the distance between the occupied sites (**I**) or used nest sites (**III**), influences both movements as well as occurrence in an urban landscape. According to the results from chapter **III**, the probability to switch nest decreased with increasing distance between the nest sites. This could be explained with structurally connected nest sites being located more often closer to each other than unconnected nest sites. However, when investigating the importance of different connectivity

measures to nest-site switching, results were varying. First, the best approximated connectivity measure that allowed routes outside home-range boundaries increased only nest-switching probability of males, which means that mature forested connections within home-range are unimportant to their nest-site switching. Second, when taking the interaction of connectivity with distance into account, switching probability gave conflicting results. The best approximated connection (nest sites were connected by suitable forests and gaps and routes outside home-range boundaries were allowed) increased and the second one (connection was by straight line by forested habitats and gaps allowed) decreased the switching probability of the males, whereas both had negative influence on the female switching probability. All this inconsistency is likely to be caused by the difficulty in measuring and defining the connectivity in a way that is relevant for a species (Bélisle 2005). In addition, other factors such as habitat selection on a larger scale or differing preferences for the nest sites might confuse my results (Johnson 1980). However, my findings indicate that structural forested connections are not a limiting factor for flying squirrel nest-site movements in an urban landscape. Indeed, even though the importance of forested connections on nest-site movements has not been studied before, the connectivity of landscape has been shown to have different effects on forest-dwelling mammals. For example, connectivity has both increased and had an insignificant effect on the probability to return home of relocated individuals (Bowman and Fahrig 2002, Smith et al. 2011). In the case of flying squirrel, management actions improving the suitability of matrix for species movements could be a more efficient conservation tool than the ones preserving forested connections (Caryl et al. 2013).

3.2. Current habitat protection fails to meet the habitat requirements of flying squirrel

Concerning the effectiveness of the flying squirrel habitat protection, we showed that the implementation of the Habitats Directive in the case of this species is unsuccessful (**II**). This contradicts both with global targets to stop the biodiversity loss, and with the conservation targets set by the European Union (Anonymous 2010). As evidence, we demonstrated that most of the forests occupied by the species are likely to be harvested so that environmental authorities are unaware of the species occurrence. In addition, we showed that despite of the delineation of breeding and resting places for protection by the authorities, they likely became abandoned. The ineffectiveness of procedure is conflicting in the sense of directed resources; a fifth of the annual species protection resources were used by the regional environmental authorities to run the practice (SYKE 2011). All this highlights the general need to study and report the true outcomes of conservation practices (Sutherland et al. 2004, Santangeli et al. 2013b).

We first estimated by means of a simulative approach that about 5.7% of the sites, where forest was logged in 2005-2012, would have been occupied by the species. Hence, when this was compared to the positive decisions made by the authorities, we concluded that only 2.7% of cases would have led to logging restrictions. This indicates that regional environmental centres that are responsible for the delineation of protected sites have insufficient information on the presence of the species, and that comprehensive survey and aggregating spatial data on different sources about the species distribution is necessary (**II**).

According to the second finding, occupancy decreased because of habitat destruction in the surroundings of delineated occupied sites. The ineffectiveness of habitat protection guidelines has been similarly confirmed in western Finland (Santangeli et al. 2013b). Together, these two studies suggest that guidelines given to preserve the occupied sites are insufficient to conservation of the species. Exact threshold for minimum required habitat area is still to be clarified, but when compared to utilized space (average home-range size by MCP for a female was 6.8 ha and by cluster analysis 3.7 ha, **III-IV**), the preserved areas end up to be excessively small. For example, an average area delineated by the authorities and saved from logging was 0.58 ha in southern and central Finland (**II**). Moreover, according to the given guidelines, protected areas can result in conserved plots as small as 0.03-0.07 ha (Anonymous 2004, Santangeli et al. 2013b). This emphasizes that in order to improve the effectiveness of conservation, significantly larger areas should be protected. However, as already currently a lot of resources are used on the habitat delineation practice, linking the flying squirrel protection with forest biodiversity conservation, or using the flying squirrel as an umbrella or surrogate species (Hurme et al. 2008b, Mortelliti et al. 2009) would be a more cost-efficient protection approach. For example, flying squirrel could be used as a surrogate together with other species, for example with raptors that inhabit mature forests in Finland (Burgas et al. 2014).

3.3. Scale-dependent responses to landscape modification

I found that landscape modification, such as creation of a large amount of low-quality sparsely forested or open areas, affects both movement activity and survival of the flying squirrel (**III**, **IV**). This is not surprising, because with habitat loss and fragmentation individuals become increasingly exposed to an unsuitable matrix (Fahrig 2003; 2007). In addition, I discovered sex-specific differences in movement patterns and in responses to landscape modification. For example, males used considerably larger areas and moved longer distances than females, and thus were more affected by the surrounding landscape features.

3.3.1. Space-use responses

In general, the presence of urban habitats on movement routes increased movement distance and movement speed (**III**). This means that as a response to the fragmentation

of suitable habitat at small scale, flying squirrels have to move longer distances to reach other mature forest fragments (Ims et al. 1993, Selonen et al. 2001). I also observed that movements were faster in response to these heavily modified habitat types. This indicates that flying squirrels are trying to minimize the time spent in low-quality habitats, likely because of low amount of resources or high predation risk or both (Schick et al. 2008). In my case, movements could be fast because individuals were moving in a familiar landscape in contrast to the other observations obtained from experimental approaches where individuals were relocated outside territories (Flaherty et al. 2008).

I found that the modification of forest landscape at large scale can impede animal movements, although this was not observed at the small-scale (**III**). Supporting this, total distances moved per night by males decreased with the amount of urban habitats within home range. However, no such an effect was found in females. Males are the more mobile sex, moving long distances (in the flying squirrel up to 2 km) in the night-time and occupying extensive home ranges (65 ha on average). However, individuals might have to spend more nights in one part of the home range before shifting across an unsuitable matrix to another suitable forest patch, because moving across inhospitable matrix can be costly. Urbanization of matrix landscape has also harmed the movements of sugar gliders (Caryl et al. 2013). Furthermore, differences between sexes are supported by the general movement behaviour and social organization of the flying squirrel, since the female is more likely to stay within one suitable forest fragment (Selonen et al. 2001). Similar social organization has found in several other arboreal squirrel species and seems to be reasonably stable despite of fragmentation (Lurz et al. 2000, Wauters et al. 2001, Taulman and Smith 2004, Verbeylen et al. 2009).

In addition to landscape factors and habitat availability, I found that home-range size affected the flying squirrel behaviour and living in chapters **III** and **IV**. For example, the number of nest sites was greater in larger home ranges and individuals that stayed alive longer utilized larger areas. This suggests that a large home-range area might be linked to a better acquirement of resources (Ims et al. 1993). Trees are important resources for flying squirrels, providing nesting cavities and food (Hanski 1998, Reunanen et al. 2002). Animals might benefit from many nest sites because of possibility to switch to next alternative nest when parasite burden in one nest gets overly high, or when the predation risk of a nest site increases (Roper et al. 2002). It is likely that flying squirrels that survived longer had time to use more extensive areas than the short-lived ones. Thus, the link between individual survival and more fine-scale habitat quality, such as the amount of available nests, their location or food resources provided (Lurz et al. 2000, Wauters et al. 2001) still needs to be confirmed.

3.3.2. Survival in modified landscapes

It is evident that habitat loss and fragmentation can reduce the survival of animal populations (Fahrig 1997, Henle et al. 2004). However, there are only a few studies on the

effects of landscape modification on individual survival in forest-dwelling mammals (but see Haapakoski and Ylönen 2010, Mortelliti et al. 2014). In the case of the flying squirrel, I found that modified and low-quality habitats in the surrounding landscape increased mortality for adult males (**IV**). In addition to being more mobile, flying squirrel males also used other habitat types than mature spruce-dominated forests more frequently than females (**III**). Thus, by utilizing unsuitable and riskier habitats, males may become more exposed to predation than females who prefer to stay within one suitable forest fragment. Similar finding has been made with field voles (*Microtus agrestis*) when males have been more likely to be caught by birds of prey than females (Koivunen et al. 1996), and with bank voles (*Myodes glareolus*) when males have performed more risk-taking behaviour in fragmented landscapes (Haapakoski and Ylönen 2010).

I found a strong regional variation in survival probabilities of the flying squirrel. The overall mortality was highest in the urban study area in Kuopio, whereas predation-caused mortality was highest in Anjalankoski. These findings are likely to be related to different local conditions, such as landscape compositions and predator densities. Previously, the survival of forest-dwelling mammals have been found to show varying patterns in urban environments as mortality has either increased or decreased. This may be due to differences in predator community structure or in traffic-related mortality rates (Ditchkoff et al. 2006, McCleery et al. 2008, McCall et al. 2010). In my study, the overall survival probability was lowest in the urban study area, but mortality was not related with urbanization *per se*. Cats preyed upon a few flying squirrels, which shows that domestic cats can cause mortality among arboreal squirrels (Gillies and Clout 2003, Woods et al. 2003). However, these events were not restricted to the urban study site only. Thus, my results altogether imply that urbanization does not increase flying squirrel mortality.

Another potential factor causing regional differences in survival is temporal and spatial variation in predation pressure. For example, Siberian flying squirrels have been more abundant in diet of birds of prey in years of high vole densities (Selonen et al. 2010). Thus, the most likely explanation for the high predation-related mortality in Anjalankoski is yearly variation in the risk to become prey. In addition, increased predation pressure at the landscape scale could be linked to the landscape structure of the site, which is heavily modified and characterized by open and sparsely forested low-quality habitats. In earlier studies, variation in flying squirrel survival and population size has been related to the region and amount of suitable habitat (Lampila et al. 2009, Koskimäki et al. 2014).

In line with my hypothesis, survival was lower in juveniles less than one year old than in adults. However, I observed that natal dispersal distance *per se* was not related to the survival probability. Thus, even long-distance dispersal (up to 8 km) did not increase mortality (**IV**). This is in contrast with the expected costs of dispersal, which are generally assumed to increase with moved distance (Byrom and Krebs 1999). My observation with the flying

squirrel could be explained by exploratory behaviour of the philopatric juveniles and short-distance dispersers (Selonen and Hanski 2006). These individuals tend to perform exploratory trips around the natal site more frequently than long-distance dispersers and during the natal dispersal period they are most likely exposed to inhospitable habitats and predation. My findings show that juvenile mortality rates are considerably high already before dispersal, which is in line with the previous findings on mortality being high in the early stage of life in many other mammalian species (Promislow and Harvey 1991, Koskimäki et al. 2014). In addition to mortality caused by predation, juveniles are likely to suffer from low survival when they practise moving outside the nest. I observed a relatively high number of death events when juveniles drowned in water bodies, which indicates that juveniles are not as good as adults in estimating their gliding distances. In conclusion, even if dispersal includes some survival costs, they are not related to the distance moved *per se* in the flying squirrel.

3.4. Effects of season

This thesis demonstrates that flying squirrel movement activity and survival are not only affected by habitat and landscape, but also by season (**III**, **IV**). Males moved faster and over longer distances especially in early spring (March to April) and in summer (July to August), whereas female movement activity consistently increased towards summer and peaked in July (**III**). For males, peaks in monthly movement distances are most likely explained with the start of the mating season when they search for females, whereas females could be able to move further after juveniles have become independent in late summer. Furthermore, individuals might have used the relatively short nights (ca 5.5 h) foraging and preparing for winter in July (Hanski et al. 2000a).

High mortality during the breeding season (April to July) seems to approximately coincide with monthly peaks in movement activity. In general, flying squirrels are unlikely limited by seasonal availability of resources, as for example the red squirrel can be (Lurz et al. 2000, Wauters et al. 2001). However, females have to forage in the daytime when they take care of the young, whereas males can be active before dusk in the mating season (Törmälä et al. 1980, Hanski et al. 2000a). Thus, the increased mortality could indicate that predation risk during the breeding period is higher because of a change in behaviour (Magnhagen 1991). Risk to be preyed during this season could also be higher because there is a large demand for food by predators that are growing their offspring. Hence, the link between increased movement activity and potential probability to be preyed in this species needs a detailed investigation in the future.

4. Conclusions

In the light of current habitat protection ineffectiveness and population decline, the future for the flying squirrel in Finland does not look promising. In my thesis, it was found that regional environmental authorities responsible for flying squirrel conservation have inadequate knowledge on its presence. In order to improve the species conservation, a more accurate database of its distribution is needed. The minimum amount of required habitat has still not been confirmed for an individual flying squirrel, but based on the results and earlier findings, protecting only a small amount of suitable forest around the occupied site is ineffective (Santangeli et al. 2013b). Thus, habitat protection could be directly improved by preserving larger mature forested areas around the occupied sites. An encouraging conclusion of my thesis is that the flying squirrel does not seem to be strongly disturbed by urbanization. Hence, protecting species in urban forests often exempt from heavy forestry management and harvesting is an interesting and likely a cost-efficient opportunity. In addition, I found that structural forested connections were not highly important and that occurrence in urban study area increased with the area of suitable movement habitat, which indicates that managing a non-habitat matrix landscape between suitable forest patches to facilitate species movements might be beneficial for species conservation in modified landscapes (Caryl et al. 2013).

In chapter **IV**, I found that juvenile flying squirrels did not suffer from high mortality in relation to dispersal distance, although costs of natal dispersal were expected to increase with distance moved. As modified habitats in the surrounding landscape increased mortality of adult males that typically move long distances, the risks of moving could be different for young and adults that are using habitats differently. It seems that movement patterns and landscape modification can have a possible joint effect on survival. In the future, a more detailed investigation on whether distances moved by adults affect flying squirrel survival or whether habitat fragmentation per se has negative survival impacts might be fruitful. Overall, results of survival indicate that there is regional differences in mortality rates related to spatial and temporal variation in predation pressure and landscape context.

The results of my thesis underline that the response of a forest-dwelling species to landscape modification depends on scale. For example, movement responses are in general diverse and plastic, but the effect of urban habitat was different on the scale of used movement routes than on the scale of entire home-range. Moreover, females and males may have different requirements for resources and space, which was demonstrated by the different effects of urban and low-quality habitats on their movement activity and survival. Varying results of the importance of forested connections indicate that measuring and defining landscape connectivity in a species-specific way is challenging in

heavily modified landscapes and that also risks and costs related to movements need to be measured (Bélisle 2005), because movements in human-modified landscapes can be risky (Fahrig 2007).

What still remains to be studied is the habitat-biased dispersal of juveniles in urban landscapes. For example; are they selecting for more urbanized landscapes than expected, or in contrast, do they tend to settle in forested areas outside cities? These research prospects would be relevant in order to develop species protection measures particularly in urban areas. Finally, it has already been demonstrated with other animals that habitat selection and home-range establishment influence individual fitness parameters such as survival and life-time reproductive success, and these ultimately affect population dynamics (Matthiopoulos et al. 2015). Thus, I propose that in addition to studying the effect of forest habitat modification only on animal space use, it would be highly important to show the effect on individual fitness. For example, it would be worthwhile to investigate the connection between habitat selection and survival or that between habitat selection and breeding performance in a modified landscape.

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